

WOODY VEGETATION AND SUCCESSION IN THE GARIN WOODS, HAYWARD HILLS, ALAMEDA COUNTY, CALIFORNIA

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ABSTRACT

Floral composition, stand structure, and successional relationships were studied in a stand of broadleaf evergreen forest in the East San Francisco Bay Hills, Hayward, Alameda County, California. Data from this study furnishes the first detailed profile of the woody plant communities in the Hayward Hills and provides a model for comparisons with other East Bay woodlands. Three main vegetational types were identified and characterized: a lower, bay (*Umbellularia californica*) woodland/forest; an upper, oak (*Quercus agrifolia*) woodland; and a central, apparently transitional oak-bay woodland; each vegetation type is defined by a distinctive tree-shrub assemblage. The author found good evidence to support McBride's (1974) paradigm of East Bay plant succession, i.e., a general movement toward a bay-dominated community and away from an oak-dominated assemblage. On the study site tree-fall of dead madrone (*Arbutus menziesii*) has opened much of the canopy and may be affecting the rate of this successional pattern.

Mixed evergreen forest is the dominant vegetation type in the hills of the eastern San Francisco Bay Area (Kuechler 1977; Sawyer *et al.* 1988). In central-coastal California north of Monterey County, this association includes *Pseudotsuga menziesii* (Douglas-fir), *Lithocarpus densiflora* (tan oak), *Quercus chrysolepis* (canyon live oak), *Aesculus californica* (buckeye), *Umbellularia californica* (bay), *Arbutus menziesii* (madrone), *Acer macrophyllum* (big-leaf maple), and *Quercus agrifolia* (coast live oak) (Munz and Keck 1959). In the East San Francisco Bay Hills, Douglas-fir and tan oak are absent (Havlik 1974); in this area the less general epithet 'broadleaf evergreen forest' is often employed (Smith 1960).

On the eastern margins of the San Francisco Bay Area, broadleaf evergreen forest stands are dominated by two species, *Quercus agrifolia*, and *Umbellularia californica*. In a study of floral community succession in the Berkeley Hills, McBride (1974) found evidence that *Q. agrifolia*-dominated oak woodland represents the climax community in areas where grazing is light and ground fires occur periodically. Given these conditions, grasses give way to *Baccharis pilularis* and associated shrubs, and these in turn are replaced by a

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coast live oak-dominated assemblage. In heavily grazed stands that are protected from fire, this oak woodland is succeeded by *U. californica*-dominated "bay woodland". Intermediate conditions favor the existence of a mixed "oak-bay woodland". In general, McBride found that modern East Bay conditions favored development of bay woodland and forest at the expense of oak-dominated communities. In this paper, woodland is defined as a tree-dominated community (>30% tree cover) with an open canopy; forest has a closed canopy.

General, qualitative descriptions of oak- and bay woodland and mixed broadleaf forest are available in Cooper (1922), Bowerman (1944), Munz and Keck (1959), McBride (1974), Griffin (1988) and Sawyer et al. (1988) etc., but few quantitative data have been published on the floristic composition, stand structure and successional trends of these vegetation types in the East San Francisco Bay Area (an exception is Wetzel (1972)). The lack of basic ecological research in the Hayward Hills was the primary motivation for the initiation of this study.

This research, conducted between January and May of 1994, sought: (1) to identify the major floristic components and stand structure of the woody plant communities in Garin Woods, a broadleaf evergreen forest and woodland in the Hayward Hills, Alameda County; and (2) to shed some light on the possible successional relationships between these communities.

Study site. The study was located at the Garin Woods ecology field station of the California State University, Hayward, Alameda County, California, approximately one kilometer southeast of the C.S.U. campus, and 10 km east of the San Francisco Bay (lat. 37°39', long. 122°2'30") (Fig. 1). Topography is hilly and locally very steep; elevations within the station property range from approximately 110 m in the Zeile Creek drainage on the west, to about 240 m on hilltops on both the north and south boundaries. The study site itself is on a north-facing slope of 35 to 45+ degrees declivity and contains approximately 7.1 hectares of broadleaf evergreen woodland and forest, and some scrubland. Grassland frames the site on both south and west.

Local geology is complex and poorly understood. Geologic mapping on land immediately adjacent to the Garin Woods field station has uncovered a complicated medley of gabbro and serpentinite, ocean sediments and metamorphic rocks, and mudstones with interbedded sandstones and limestone nodules; local hilltops (and most of the study site) are the Quaternary Leona Rhyolite (Robinson 1956; Dibblee 1980).

The Garin Woods are located wholly within the Altamont-Diablo soil association, which is composed of moderately sloping to very steep, brownish and dark-gray, moderately deep soils; parent ma-

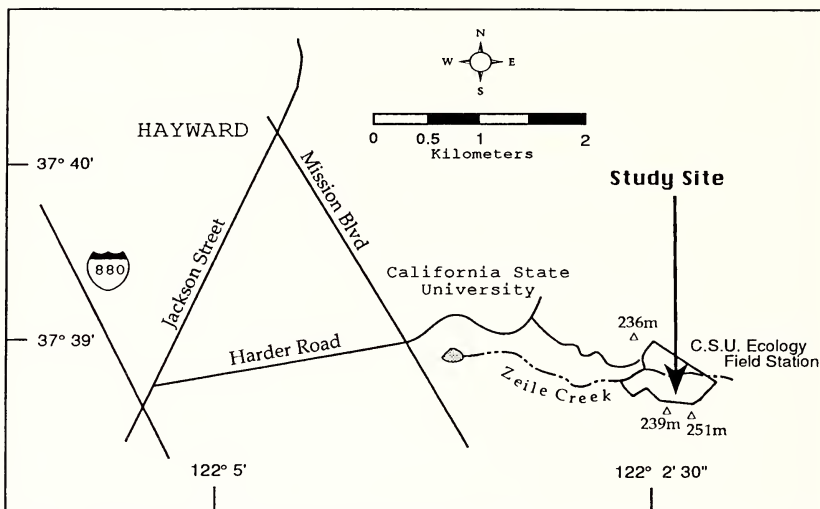


FIG. 1. Study site location. The site itself is located on a north-facing slope south of Zeile Creek (arrow).

terial is primarily soft sedimentary rock. The study site itself is found almost entirely on the Los Gatos-Los Osos Complex of loam and silty clay loam. Woodland edges and surrounding grassland are on the Altamont rocky clay, a moderately deep soil found on more shallowly sloped (7–30%), mostly south-facing slopes (Soil Conservation Service 1966).

Local climate is mediterranean, with cool, humid winters and warm, dry summers. Climatic data for the study site is unavailable, but extrapolation from regional isotherm maps yields a mean annual temperature of approximately 14.5°C, a maximum monthly mean of 24°C in July and a minimum monthly mean of 4°C in January. Annual precipitation averages approximately 545 mm, with 85% falling between November and April. Winds are predominantly from the north west and the west (A.B.A.G. 1974).

The study site, privately owned prior to its sale to the university, has been protected from fire for most of the last century. Intermittent livestock grazing occurred on the property until approximately 15 years ago. Cattle grazing continues south of the study site in Garin/Dry Creek Pioneer Regional Park. Fences separating the two properties are in poor condition and minor incursions of livestock onto university property occur from time to time. The present intensity of deer grazing is difficult to establish; the author's observations suggest that at least a half-dozen mule deer (*Odocoileus hemionus*) regularly feed in the area, and that browsing is locally heavy.

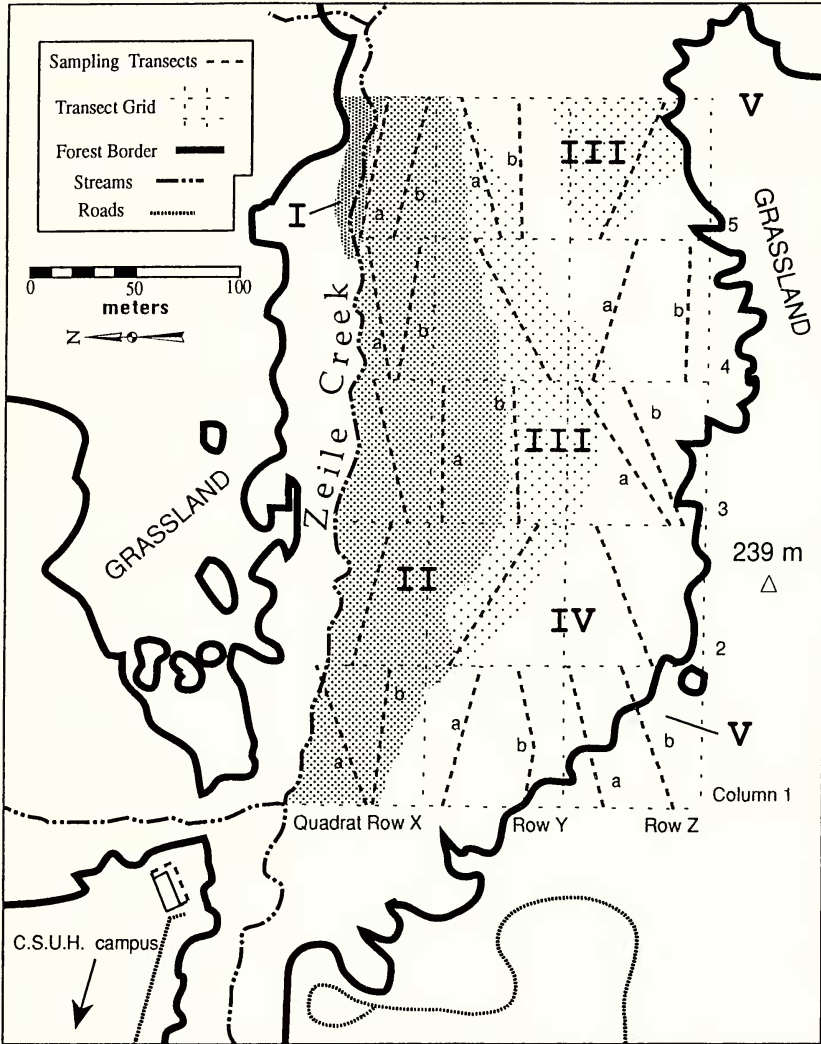


FIG. 2. Study site, with sampling quadrats (transect grid) and transect locations, and approximate boundaries of the woody vegetation types discussed in this paper. I) riparian woodland; II) bay woodland; III) oak-bay woodland; IV) oak woodland; V) *Artemisia*-grassland scrub.

MATERIALS AND METHODS

Data collection. The forest vegetation was sampled along 24 transects between January and April, 1994, using the point-centered quarter method (Cottam and Curtis 1956). In this method, random points are chosen along a transect, the area around each point is

divided into four 90 degree quarters, and the nearest tree (or shrub) in each quarter is sampled.

Preliminary field reconnaissance suggested the existence of three fairly distinct woody plant assemblages grading from the base of the hill to near the summit, therefore a stratified-random sampling scheme was employed to maximize sampling precision. Transect placement was determined using a grid of 15 75 m \times 75 m quadrats (3 north-south \times 5 east-west) overlaid on the U.S.G.S. 7.5-minute Hayward Quadrangle map (Fig. 2). Nine quadrats to be sampled were randomly chosen, three from each of the three north-south quadrat-rows. Two sampling transects were placed on the map in each chosen quadrat by randomly choosing two points (figured in meter distances) along the east and west sides of each selected quadrat, and then connecting the northernmost points on east and west to form transect 1; transect 2 was drawn between the southern points. A preliminary estimate of sample size requirement was made using Seber's formula for plotless sampling methods (Krebs 1989).

When half of all planned transects had been run, distance data were analyzed for distributional pattern using POISSON and NEG-BINOM (Krebs 1989). This analysis showed that the vegetative pattern was aggregated ($k = 10.08144$, standardized Morisita Coefficient = 0.5001). Taking this aggregation into account, an updated computation of sample size requirement was made using SAMPLE (Krebs 1989), and necessitated one additional sampling transect within each vegetative type. Since there were two unsampled quadrats remaining in each quadrat-row, I decided to run one extra transect in each, so as to maximize coverage of the study site. Ideally, two transects would have been sampled in all of the quadrats, but time constraints did not permit this.

Point-centered quarter transect lines were coursed using the field map, compass triangulation and paced measurements. At randomly chosen intervals (at least seven meters apart to avoid sampling the same plant twice) distance was measured, height estimated, and species type noted, for the nearest canopy member (defined as any woody plant ≥ 2 meters in height receiving direct, overhead sunlight) and the nearest 'middle story' member (defined as woody plants ≥ 2 meters in height not comprising part of the canopy, i.e., existing in the shade of a larger neighbor) in each 90° quarter. Every transect included at least seven sampling points.

Diameter at breast height (dbh) measurements were not taken in the initial survey—the author was originally interested only in species diversity and floristic composition—but the obvious effects of local madrone mortality and competition between both canopy and middle story species on present stand composition and structure underlined the importance of this data to any interpretation of the present situation in the Garin Woods. Therefore, in May, 1994, four additional point-quarter transects were sampled, across the study

site from east to west, to measure dbh of the canopy tree species. The transects were regularly spaced so as to maximize coverage of each of the vegetation types. One dbh measurement was made of the nearest specimen of each canopy species in every quarter, except in the case of *Arbutus menziesii*, where every specimen sighted (dead or alive, standing or fallen) was measured for dbh.

Data analysis. Point-quarter data from 24 transects were compiled and analyzed for mean point-to-plant distance, relative densities (percentage of sampled stand), and total density using QUARTER (Krebs 1989).

Indices of dispersion were calculated by dividing the variance of point-to-nearest neighbor distances for each vegetation type by the mean point-to-nearest neighbor distance ($\text{var.}/\bar{x}$).

Vegetation types and plant community relationships were noted in the field and clarified by tabling and plotting relative density data. Key inter- and intracommunity relationships were identified and correlated using REGRESS (Krebs 1989). Using these indicator relationships, the proportions of *U. californica* vs. *Q. agrifolia* in the canopy, and field observations, each transect was assigned to one of three vegetation types: bay woodland and forest, oak-bay woodland, or oak woodland.

Size-frequency data were compiled and plotted to provide further evidence for climax vegetation types and successional relationships between the species of the Garin Woods canopy.

Species nomenclature follows Hickman (1993).

RESULTS

Woody plant communities. Field experience and the data collected through point-quarter sampling elucidated five major woody plant communities on the study site: bay woodland and forest, oak-bay woodland, oak woodland, riparian woodland, and *Artemisia*-grassland scrub. This study was directly concerned with the three broadleaf evergreen communities but some transect lines crossed riparian woodland and *Artemisia*-grassland scrub as well. Table 1 outlines the characteristic floral components of the five woody vegetation types.

Stand structure. Data from the 24 point-quarter transects are shown in Table 2, and in Figure 3. Assignment of transects to the three broadleaf vegetation types was made using the following criteria:

- 1) Relative proportions of *U. californica* vs. *Q. agrifolia* in the canopy.
- 2) Floristic composition and stand structure of the middle story (see below).
- 3) Field observations.

TABLE 1. WOODY VEGETATION TYPES IN THE MAIN GARIN WOODS, C. S. U. H. RESEARCH FOUNDATION ECOLOGY FIELD STATION, HAYWARD HILLS, ALAMEDA COUNTY, CALIFORNIA.

Vegetation type	Site description	Area	Dominant species	Associated species
Riparian Woodland	Streambank and alluvial terraces, NE corner	0.1 ha	<i>Salix lasiolepis</i> <i>Salix laevigata</i> <i>Acer macrophyllum</i>	<i>Prunus virginiana</i> <i>Cornus sericea</i> ssp. <i>sericea</i> <i>Baccharis pilularis</i> <i>Heteromeles arbutifolia</i> <i>Corylus cornuta</i> var. <i>californica</i> <i>Quercus agrifolia</i> <i>Arbutus menziesii</i> <i>Acer macrophyllum</i>
Bay Woodland/Forest	Steep slopes (40–50 deg.) on lower hillside, N facing	2.8 ha	<i>Umbellularia californica</i>	<i>Toxicodendron diversilobum</i> <i>Holodiscus discolor</i> <i>Heteromeles arbutifolia</i> <i>Arbutus menziesii</i> <i>Garrya elliptica</i>
Oak-Bay Woodland	Moderately sloped, discontinuous along center of hill, N facing	1.4 ha	<i>Quercus agrifolia</i> <i>Umbellularia californica</i>	<i>Toxicodendron diversilobum</i> <i>Holodiscus discolor</i> <i>Heteromeles arbutifolia</i> <i>Arbutus menziesii</i> <i>Garrya elliptica</i>
Oak Woodland	Moderately to shallowly sloping, upper hillside to ca. 230 m, N facing	2.9 ha	<i>Quercus agrifolia</i>	<i>Toxicodendron diversilobum</i> <i>Umbellularia californica</i> <i>Holodiscus discolor</i> <i>Ribes</i> spp.
(Oak Woodland-Grassland Ecotone)	0–25 m wide, bordering Oak Woodland on SW, mostly W facing	—	Stunted <i>Q. agrifolia</i> and <i>U. californica</i>	<i>Quercus garryana</i> × <i>durata</i> <i>Quercus durata</i> <i>Rhamnus crocea</i> <i>Mimulus aurantiacus</i> <i>Quercus palmeri</i>
<i>Artemisia</i> -Grassland-Scrub	W and S edges of study site	0.2 ha	<i>Artemisia californica</i>	<i>Lupinus albifrons</i> var. <i>collinus</i> Various perennial grasses

TABLE 2. QUANTITATIVE DATA FOR WOODY PLANTS OF THE CANOPY AND MIDDLE STORY IN THE GARIN WOODS. Species observed but not sampled are indicated by (x). For transect location see Figure 2.

Transects	Bay woodland X1a, X1b, X2, X3, X4a, X4b, X5a, X5b, Y3a	Oak-Bay woodland Y2, Y3b, Y4, Y5a, Z5	Oak woodland Y1a, Y1b, Y5b, Z1, Z2, Z3a, Z3b, Z4a, Z4b	Study site totals
Approximate sampled area (hectares)	2.8	1.4	2.9	7.1
Canopy				
Total sample size	177	95	155	427
Index of dispersion (var./ \bar{x})	1.80	1.52	1.31	
Density (/hectare)	247.6	300.4	369.9	
Density 95% C.L.	213.3–286.7	244.9–366.9	315.4–432.6	
Relative density of canopy species (%)				
<i>Acer macrophyllum</i>	2.9	1.1	0.0	1.4
<i>Alnus rhombifolia</i>	0.6	0.0	0.0	0.2
<i>Arbutus menziesii</i>	8.5	7.4	0.0	5.2
<i>Garrya elliptica</i>	0.0	0.0	1.9	0.7
<i>Heteromeles arbutifolia</i>	0.0	0.0	0.7	0.2
<i>Prunus virginiana</i>	0.6	0.0	0.0	0.2
<i>Quercus agrifolia</i>	15.3	48.4	69.0	42.1
<i>Quercus chrysolepis</i>	x	0	0	—
<i>Quercus palmeri</i>	0.0	2.1	0.0	0.5
<i>Quercus garryana × durata</i>	0.0	0.0	5.8	2.1
<i>Salix lasiolepis</i>	0.6	0.0	0.0	0.2
<i>Umbellularia californica</i>	71.2	41.1	22.6	46.9
Middle story				
Total sample size	178	95	154	427
Index of dispersion (var./ \bar{x})	2.00	0.70	1.44	
Density (/hectare)	381.7	1173.4	855.9	
Density 95% C.L.	326.1–445.4	956.6–1432.9	729.5–1001.4	
Relative density of middle story species (%)				
<i>Acer macrophyllum</i>	1.7	0.0	0.0	0.7
<i>Artemisia californica</i>	0.0	0.0	0.7	0.3
<i>Baccharis pilularis</i>	0.0	1.1	0.7	0.5
<i>Cercocarpus betuloides</i>	0.0	0.0	0.7	0.3
<i>Cornus sericea</i> var. <i>sericea</i>	1.1	0.0	0.0	0.5
<i>Corylus cornuta</i>	13.5	4.2	x	6.6
<i>Garrya elliptica</i>	0.6	6.3	1.3	2.1
<i>Heteromeles arbutifolia</i>	34.3	11.6	4.6	18.5
<i>Holodiscus discolor</i>	4.5	15.8	13.6	10.3
<i>Mimulus aurantiacus</i>	0.0	1.1	1.3	0.7

TABLE 2. Continued.

Transects	Bay woodland	Oak-Bay	Oak woodland	Study site totals
	X1a, X1b, X2, X3, X4a, X4b, X5a, X5b, Y3a	woodland Y2, Y3b, Y4, Y5a, Z5	Y1a, Y1b, Y5b, Z1, Z2, Z3a, Z3b, Z4a, Z4b	
<i>Oemleria cerasiformis</i>	x	1.1	1.3	0.7
<i>Quercus agrifolia</i>	5.0	1.1	5.8	4.4
<i>Quercus durata</i>	0.0	0.0	1.3	0.5
<i>Quercus palmeri</i>	0.0	2.1	x	0.5
<i>Rhamnus californica</i>	1.1	x	1.3	0.9
<i>Rhamnus crocea</i>	0.0	0.0	0.7	0.2
<i>Ribes</i> spp.	x	1.1	5.2	2.1
<i>Sambucus mexicana</i>	x	x	x	—
<i>Toxicodendron diversilobum</i>	5.0	26.3	44.8	24.1
<i>Umbellularia californica</i>	33.1	28.4	16.2	26.0

Criterion 2 involved a series of comparisons. In the Garin Woods *Toxicodendron diversilobum* (as a shrub ≥ 2 m) exhibits a very low affinity for stands dominated by *U. californica*. Correlation of data combined from all three vegetation types showed that this negative relationship is statistically significant (Fig. 4a), and it was thus taken as a fairly reliable measure of the vegetation type. (Pooling data from three different sampling strata raises valid questions regarding the statistical independence of those data points found within each respective stratum: in this paper, Figures 4a and 4b are employed only to illustrate an important ecological reality—for my present purposes the causes of this reality are immaterial.)

Other members of the middle story were also found to exhibit important vegetation-type affinities, for whatever reason: *Heteromeles arbutifolia* is the most common middle story member in bay woodland/forest, but it was not sampled on any of the transects from transect-row Z (except for Z5), which is primarily oak woodland (see Fig. 4b); *Corylus cornuta* showed a similar pattern. *Holodiscus discolor* occurred most commonly along the middle of the hill, under the often open canopy of the oak-bay woodland. Middle story density (individuals/hectare), and indices of dispersion for both the canopy and middle story were also considered meaningful gauges of vegetation type.

Succession. Data from the diameter-breast-height (dbh) measurements for Garin Woods as a whole are shown in Figure 5. *U. californica* shows the reverse J curve considered indicative of climax species (note the variation in the 21–25 cm size-class however). Figure 3b portrays the relative density of *U. californica* within the

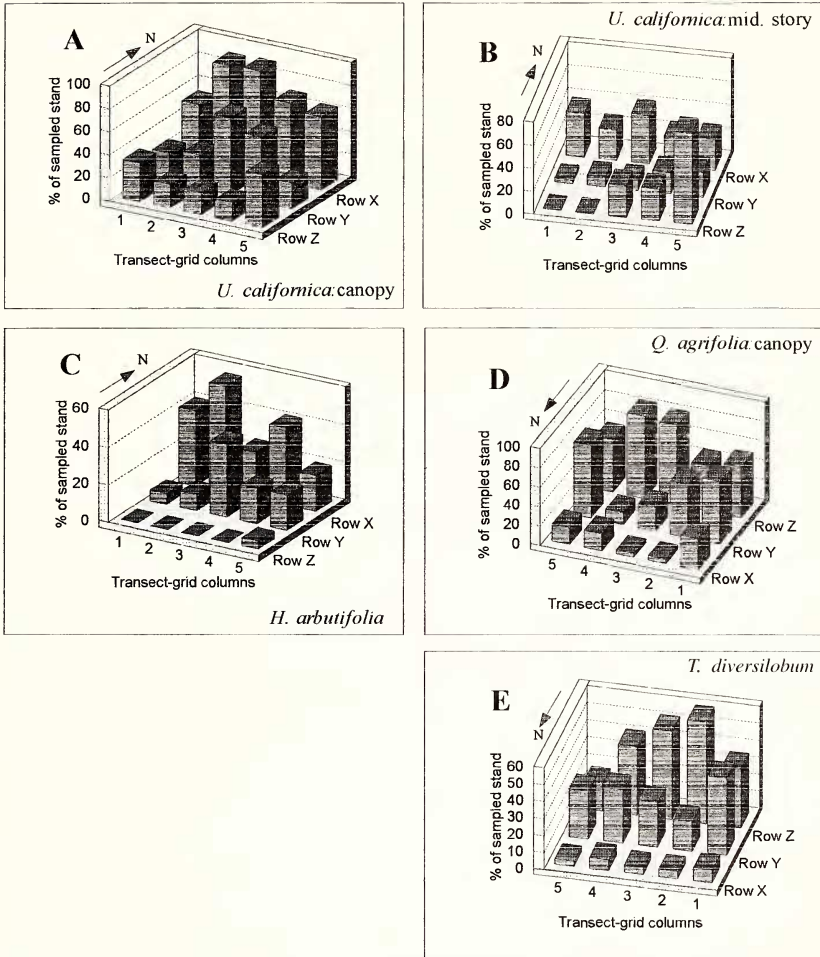


FIG. 3. Three-dimensional histograms of the distributions of selected woody species on the study site. Columns and Rows correspond to the quadrats in Figure 2. Each bar represents an approximation, derived from either one or two sampling transects (see Figure 2), of the relative frequency of each species in each quadrat. Note that Figures 3A through C are oriented 180° from Figures 3D and E. A) *Umbellularia californica*: canopy; B) *U. californica*: middle story; C) *Heteromeles arbutifolia*; D) *Quercus agrifolia*: canopy; E) *Toxicodendron diversilobum*.

middle story of each quadrat, i.e., the relative numbers of saplings and small trees within each stand. Taken together, Figures 3a, 3b and 5 point to the existence of different stands in various stages of successional progression within the Garin Woods; some are obviously older stands, with relatively little recruitment of *U. californica*

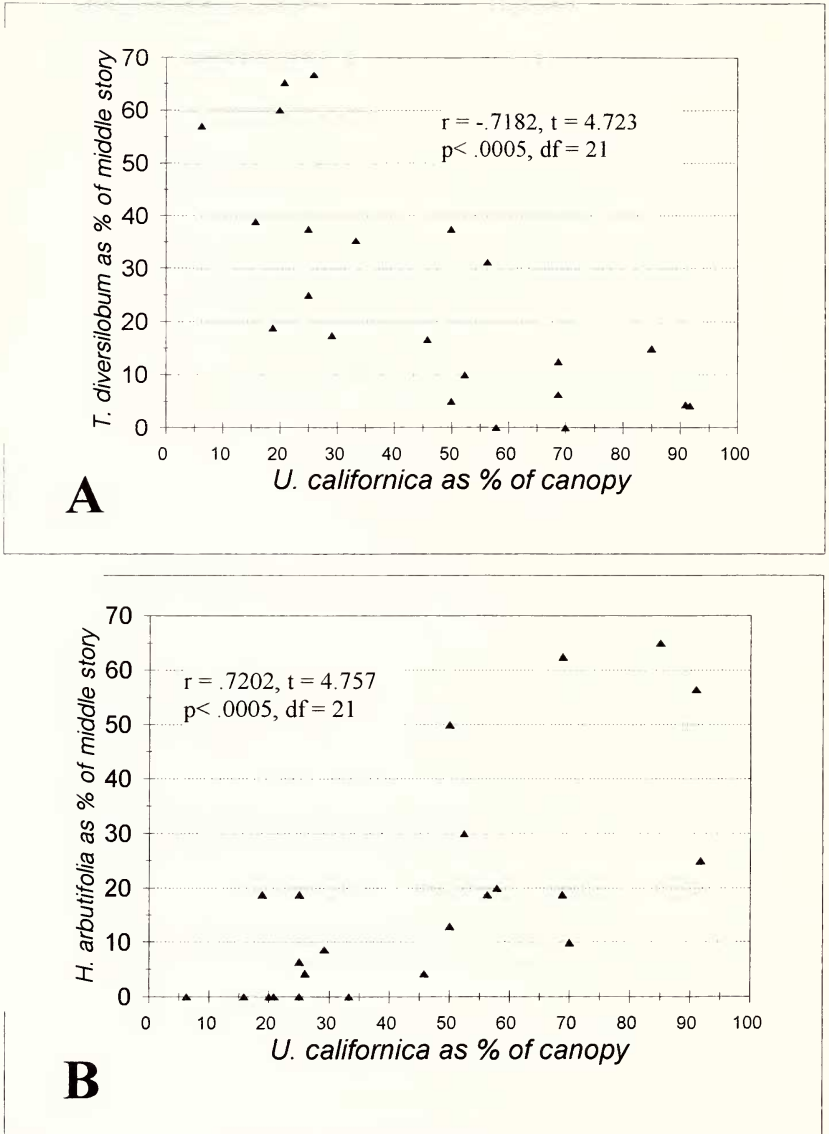


FIG. 4. A) Correlation of *Toxicodendron diversilobum* as a component of the middle story versus *Umbellularia californica* as a component of the canopy; B) Correlation of *Heteromeles arbutifolia* as a component of the middle story versus *U. californica* as a component of the canopy.

(Y3), while others (Z5) have fewer mature individuals and abundant recruitment; a few stands (X2, X3) seem to have ample recruitment even though their canopies are already $>90\%$ *U. californica*.

Figure 5 also shows size-frequency data for *Q. agrifolia* and *A.*

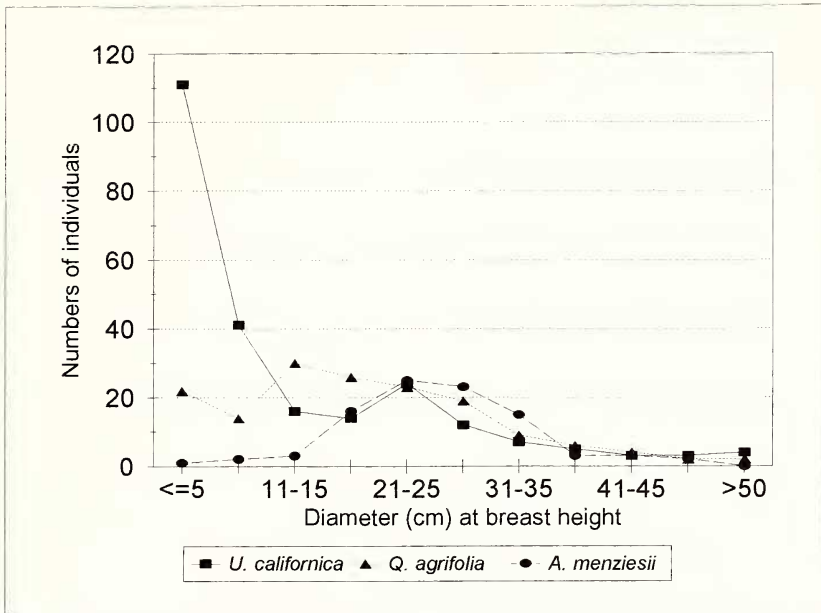


FIG. 5. Size-class data for *Umbellularia californica*, *Quercus agrifolia* and *Arbutus menziesii* in the Garin Woods. Both live and dead specimens of *A. menziesii* are included.

menziesii. There is little recruitment of *Q. agrifolia* in the Garin Woods. In fact, of the 22 measured individuals ≤ 5 cm in diameter, 9 occurred along a man-made trail in the bay woodland, 11 were in the tree-fall-caused clearings in the center of the hill, and only 2 were encountered in oak woodland.

The four dbh transects uncovered no evidence of recruitment of *A. menziesii*—the only sapling located was a trunk-sprout from a fallen individual.

DISCUSSION

Bay woodland-forest. The bay woodland-forest of the lower hill and stream bank appears to represent the local climax community, or at least a preliminary version of it. Quantitatively, the most reliable evidence for this are the size-frequency data, which suggests that *Umbellularia californica* is the only major canopy member presently replacing itself in any numbers (Fig. 5). Although aerial photo comparisons could (ideally) provide more direct evidence for the scale and the rate of transition, the scope of this study did not permit the close scrutiny of aerial photos except for use as an aid in the determination of approximate contemporary vegetation type boundaries and areas.

A generalized vegetation map of the Garin Woods, compiled by

Rowlett in 1971, hints at the changes a quarter-century has wrought in the stands along Zeile Creek: her map shows at least a half-dozen *Alnus rhombifolia* and many *Acer macrophyllum* along the stream, and a large thicket of *Salix* spp. on the north bank just within the eastern boundary of the Ecology Field Station property. Field checking in 1994 found only one surviving *A. rhombifolia*, riparian stands of *A. macrophyllum* depleted by about 25%, and only two small specimens of *Salix lasiolepis* in place of Rowlett's thicket. Although *Alnus* spp. are intolerant of aggressive competition (Fowells 1965), fluvial downcutting may actually account for much of this change: trunks of both *A. rhombifolia* and *A. macrophyllum* (among other species) are found in the creek bed, and many other streamside trees are presently being undercut. The Zeile Creek stream bed is locally entrenched up to 2.5 m, a recent occurrence common to many East Bay streams, regardless of watershed urbanization (Rogers 1988); grazing in Garin/Dry Creek Pioneer Regional Park, and housing construction within the Zeile Creek watershed have almost certainly increased sediment load and peak flow amounts, increasing the local rate of streambank erosion and causing heavy siltation at Zeile Creek's mouth in Cemetery Pond (R. Benseler and R. Tullis, personal communication). Today, bay woodland covers almost the entire south bank of Zeile Creek within the study site. Some of these streamside stands are more than 90% *U. californica*, yet recruitment is still relatively high. The five point-quarter transects run closest to the creek showed a average of 39% *U. californica* in the middle story (compared with 3% *Q. agrifolia*).

The occurrence of several small, isolated specimens of *Quercus chrysolepis* may also provide some clues as to the successional history of the Garin Woods. These individuals occur under a closed canopy of *U. californica*, in association with *Heteromeles arbutifolia*, at an altitude of 150 m (50 m below the species' published range in the Jepson Manual). There are several defoliated boles nearby which resemble *Q. chrysolepis* as well. In the Carmel Valley (south of the Bay Area), Griffin (1974) noted a *Q. chrysolepis*-phase of mixed evergreen forest in shady canyons and on steep north-facing slopes. Canopy cover was dense, understory growth was light, and colonies of *U. californica* were scattered throughout the stand. With the dominant trees reversed, this description sounds much like the lower Garin Woods. Although these exotic *Q. chrysolepis* may be just that, one wonders if perhaps they (and *H. arbutifolia*—see below) are remnant flora from a more favorable climate, or grazing/fire regime?

The bay woodland vegetation type exhibits the lowest canopy and middle story densities in the Garin Woods, and the canopy is more dominated by a single species than in either of the other two broad-leaf evergreen vegetation types (Table 2). As is common under *U. californica*-dominated canopies, the shrub layer is not well-devel-

oped (Cooper 1922; McBride 1974), and many of the shrub types are present in only one or two localities (*Salix* spp., *Garrya elliptica*, *Holodiscus discolor*, e.g.), where sufficient light reaches the forest floor and along the stream bank. The moist, low-light microclimate that results from this high, often closed canopy favors instead the growth of understory species such as *Polystichum munitum*, *Smilacina* spp., and *Disporum hookeri* (personal observation). Middle story complexity increases significantly with changes in aspect, and/or thinning of the canopy: the highest middle story densities in the bay woodland (>twice the average) are found along the western border, where the stand is more open to wind and afternoon sun and *Quercus agrifolia* comprises more of the canopy.

The index of dispersion ($\text{var.}/\bar{x} = 1.803$) for the bay woodland vegetation type shows that canopy members are highly clumped in this stratum. This is hardly surprising, since *U. californica* commonly reproduces through sprouting and vegetative propagation, creating multi-stemmed clumps, especially where there are canopy openings to the side (Stein 1958). The middle story showed even more significant aggregation than the canopy ($\text{var.}/\bar{x} = 1.999$). This would be expected in a community where canopy cover is high, and shafts of light reaching the ground are few and far between—precisely the situation in much of the lower Garin Woods.

The middle story in the bay woodland/forest is dominated by *Heteromeles arbutifolia* (toyon), which, unlike the other shrubs, is spaced relatively regularly throughout the vegetation type. This association with *U. californica* in a damp, low-light microclimate was not expected. *Heteromeles arbutifolia* is customarily associated with chaparral, or the drier, brushy edges of local forests and woodlands (Munz and Keck 1959; Ferris 1968), yet in the Garin Woods it was only infrequently encountered outside of bay woodland, and almost never seen in oak woodland (although field observations show it is common in the narrow oak woodland/grassland ecotone found along the western edge of the Garin Woods) (see Fig 3c). The elevated presence of toyon in the bay woodland could be explained in a number of ways. Field observations turned up very few *H. arbutifolia* seedlings or saplings, and many of the adult plants in the bay woodland are not healthy. Possibly, it is remnant of an earlier, more *Quercus*-dominated forest and has survived by default as middle story competition (especially from *T. diversilobum*) is essentially nonexistent, or because it has higher tolerance for the shade (and allelochemicals?) of the *U. californica*. It may also be that *H. arbutifolia* is more amenable to moist, shaded conditions than is commonly supposed: the author's observations suggest that *H. arbutifolia* is present in similar proportions in other, nearby stands of bay woodland; McBride (1971) found *H. arbutifolia* associated with moister, closed-canopy conditions, and in another study (1974) he

encountered no *H. arbutifolia* in any of the oak woodland he surveyed, yet it was a fairly common member of bay woodland stands.

Oak-bay woodland. To a certain extent, the small area classified as oak-bay woodland represents an agglomeration of more-or-less contiguous transects that do not obviously belong to either bay- or oak woodland. A strict definition of this zone is problematic, but some generalizations can be made about this vegetation type in the Garin Woods: 1) neither *Umbellularia californica* nor *Quercus agrifolia* clearly dominates the canopy; 2) canopy cover is locally sparse, or absent; 3) middle- and understory cover is dense; 4) species diversity, especially within the understory (personal observation), is high.

Field observation and data collected through point-centered quarter sampling suggest that the oak-bay woodland in the Garin Woods is more a transitional ecotone than a stable community. Canopy tree density was intermediate between the other two broadleaf evergreen vegetation types, but middle story density was >three times higher in the oak-bay woodland than in bay woodland, and 50% higher than in oak woodland (Table 2). The indices of dispersion for the oak-bay woodland provide further quantitative testimony to the transitional nature of this area. The canopy here is more random than that along the lower hill, yet more aggregated than that on the upper hill ($\text{var./x} = 1.52$). This is probably due to the more even proportions of *Q. agrifolia* and *U. californica* in this stratum. The measurement of dispersion for the middle story is extremely low ($\text{var./x} = 0.70$) (recall that 1 theoretically implies randomness, values >1 point to clumping, and <1 suggests a trend toward uniform distribution). Much of the canopy along the middle hill is open, allowing the growth of locally dense patches (scrub islands) of *Toxicodendron diversilobum*, *Holodiscus discolor*, *Ribes* spp., *Garrya elliptica*, and *Baccharis pilularis*. The cause for this is almost certainly the collapse of the local population of *Arbutus menziesii*.

Arbutus menziesii (madrone) comprised significantly more of the local tree canopy in the 1960's than it does today (R. Baalman, personal communication). Recent mass dyings have opened much of the Garin Woods' canopy, especially in the center of the hill. During point quarter and dbh sampling the author noted literally dozens of downed *A. menziesii* between transects Y2a and Y5b. Those remaining are often greatly defoliated and in the process of being overtopped by neighboring *U. californica*. Size-frequency measurements of both live and dead madrone produced a classic 'inverted bowl,' characteristic of species showing no recruitment (Fig. 5). It should be noted that this development is part of a wide regional trend. Madrone pathogens include trunk cankers, leaf galls and spots, and a spot anthracnose (Horst 1979) but the culprits most respon-

sible for this mortality have yet to be identified. Declining rainfall and higher temperatures are implicated in some circles (Benseler personal communication), but this seems unlikely, as *A. menziesii* grows best where summer soil moisture is low, and is even classified as drought resistant by the U.S.F.S. (Fowells 1965). Pelton (1962) found that seedling survival rates of madrone were extremely low, particularly in shaded conditions. In Pelton's study root-fungus and soil-dwelling invertebrates were implicated in about 60% of seedling mortality; drought *per se* accounted for 10% of seedling deaths. Madrone is often characteristic of secondary growth after logging or fire, especially from stump sprouts (Metcalf 1966); local conditions certainly do not presently favor this kind of growth. Field observations turned up only one *Arbutus* sapling in the entire Main Woods, sprouting from the cut stump of a tree that had fallen across a trail. At present *A. menziesii* comprises approximately 8.5% of the lower, bay woodland canopy, and about 7.4% of the higher oak-bay woodland: indications are that this proportion was greater in the past, and will be lower in the future.

The rapid disappearance of *Arbutus menziesii* from local forests and woodlands has important implications for the rate and direction of succession in parts of the Garin Woods. Islands of scrub presently fill many of the larger gaps created by *A. menziesii* treefall. Ground cover of *T. diversilobum*, *Rubus ursinus*, and *H. discolor* is locally very dense, and shrubby species like *Quercus palmeri* and *Baccharis pilularis* may reach heights of 4 m. Size-frequency measurements taken along the middle hill showed these open areas are fertile ground for recruitment of canopy species: 50% of all *Quercus agrifolia* seedlings sampled in Garin Woods occurred in these 'scrub islands,' as did >40% of all *Umbellularia californica* seedlings, and the only *Arbutus menziesii* seedling. Paradoxically, these openings in the canopy not only provide greater access to light and precipitation, but the well-developed shrub layer (in what has been called a nurse-plant relationship) affords better protection from predators and competing species, and helps to moderate climatic extremes (Callaway and D'Antonio 1991). This shrub layer is essentially absent in the bay woodland, and only moderately well-developed in the oak woodland. Taking into account that *U. californica* seedlings are still more than four times as common as *Q. agrifolia* seedlings in the oak-bay woodland, succession to a bay-dominated community appears to be inevitable, but indications are that transition to bay woodland has been significantly slowed by *A. menziesii* treefall.

Oak woodland. *Quercus agrifolia* is the dominant canopy species in this vegetation type; other oak members occur in the middle story of the scrubby woodland-grassland ecotone on the Garin Woods' southwestern edge. These include *Q. durata*, *Q. palmeri*, and a num-

ber of conspicuous hybrids, including a small (4–5 m), deciduous tree which occurs in a series of isolated copses ranged along the inner boundary of the ecotone. These are probably *Q. garryana* × *durata* (J. Tucker personal communication). The identification of *Q. durata* and *Q. palmeri* in the Garin Woods (confirmed by J. Tucker) represents a range extension for both species.

Indices of dispersion in the oak woodland are the most even in the Garin Woods (canopy = 1.31, middle story = 1.44). This can be accounted for by the stand habit of *Quercus agrifolia*, which is much less aggregated than that of *U. californica*, and the more open canopy of oak woodland, which allows for more middle- and under-story growth as well. *Toxicodendron diversilobum* and *Holodiscus discolor* blanket this stratum and are locally found in nearly impenetrable thickets; *T. diversilobum* is by far the dominant shrub in the oak woodland (Fig. 3e). *Heteromeles arbutifolia* and *Corylus cornuta* were only rarely encountered in point-quarter sampling: not a single example of either was sampled from the oak woodland portion of quadrat-row Z (although the author has seen a handful of each). The paucity of *H. arbutifolia* was unexpected: possibly it does not successfully compete with *T. diversilobum* in this environment.

Recruitment of *Quercus agrifolia* in the Garin Woods seems much too low to maintain the present adult population. Although the open canopy of conspecific adults and the relatively well-developed layer of nurse shrubs provide a healthy environment for seedling and sapling growth, recruitment of coast live oak in the oak woodland is practically nonexistent. On transects in this stratum, *Q. agrifolia* made up merely 5% of the middle story, and dbh sampling found only two saplings of ≤ 5 cm diameter (from 50 total samples). In contrast, 16% of the oak woodland middle story is constituted by *Umbellularia californica*, a figure with great portent for the future of this vegetation type.

Oak woodland/grassland ecotone. Floristically, the oak woodland-grassland ecotone is one of the more intriguing plant associations in the Garin Woods. The canopy in this zone is composed of stunted *Q. agrifolia* and *U. californica*, in more even proportions than elsewhere in the oak woodland, with the deciduous *Quercus* hybrid comprising the remaining 10%. Canopy height is noticeably less than within the oak woodland proper. Woody species found in this ecotonal strip which were not sampled or seen elsewhere in the oak woodland include: *Artemisia californica*, *Baccharis pilularis* (rare), *Quercus durata*, *Quercus palmeri*, *Rhamnus crocea*, and the various *Quercus* hybrids. Woody species which are significantly more common in the ecotone than in the oak woodland are *Garrya elliptica*, *Heteromeles arbutifolia*, *Mimulus aurantiacus*, and *Oemleria cerasiformis*. This ecotone apparently owes its existence to its west-

facing aspect and highly-exposed position, on the windward edge of the Garin Woods, atop a steep, 50 m high escarpment (thought to be the footwall of the West Chabot Thrust Fault by Dibblee (1980)). Wind-shearing has misshapen all of the exposed plants. An edaphic derivation for the ecotone has been postulated as well (R. Baalman, personal communication). Serpentine is known to occur along the northern continuation of the escarpment ridge, across Zeile Creek, and geologic maps suggest a continuation of this rock unit (the Coast Range Ophiolite sequence) into the western portions of the Garin Woods, but I (a geologist by training) found greatly altered basalt and rhyolite in the ecotone, but no obvious evidence of serpentine or allied minerals. More study is needed of this ecotonal community and the abiotic factors that influence it: the presence of *Quercus durata* suggests that serpentine may be one of those factors.

CONCLUSION

Evidence from all over California suggests that the present range of many oak species is shrinking (Griffin 1971; McBride 1974; Muick and Bartolome 1987; Callaway and D'Antonio 1991). Reasons for this decline may include changing climate, increased land development (Barrett 1979), changes in fire and grazing patterns (McBride 1974), and increased seedling predation by animals (Barrett 1979; Griffin 1979).

Cattle have not had access to the C.S.U.H. ecology field station for approximately 15 years, but the station's proximity to the Garin/Dry Creek Pioneer Regional Park means that a large and protected deer population may seasonally migrate in and out of the property. Browsing by livestock and deer may be the most significant impediment to oak regeneration in California (Barrett 1979). Grazing of coast live oak water shoots is locally heavy in the Garin Woods; the author noted heavily pruned *Q. agrifolia* even during the wet spring of 1994, when grass and forb availability was still high. Along the southern edge of the oak woodland, many coast live oak shrubs have been severely stunted by browsing as well. In addition to seedlings and water shoots, deer eat acorns as well (Barrett 1979, Griffin 1979); cattle also have enormous appetites for them (Duncan and Clawson 1979). Pocket gophers (*Thomomys bottae*), gray squirrels (*Sciurus griseus*), the dusky-footed wood rat (*Neotoma fuscipes*), scrub jays (*Aphelocoma coerulescens*) and the California quail (*Lophortyx californicus*), all of which are found on the study site, are other major consumers of oak acorns (Griffin 1979).

Fire is actively suppressed on the study site and in most of the increasingly populated Hayward Hills. Probably no major burn has occurred in at least the last 50 years, and possibly within this century. McBride (1974) found that the frequency of fire is one of the major

determinants of the relative proportion of oak and bay in the broad-leaf evergreen forests. *Quercus agrifolia* is extremely fire resistant (Plumb 1979), but this adaptation is of little use in the present fire regime. The present lack of recurrent fire, and the heavy grazing of oak seedlings and acorns favors *Umbellularia californica* and its young which, unlike oak, germinate well under canopies of either species (Jackson 1973).

Evidence presented in this paper suggests that the oak woodland of the Garin Woods is a remnant of a formerly more extensive vegetation type. Barring a resumption of regular ground fire and a sudden cessation of browsing and acorn predation however, it would appear that much of the study site that is not already bay woodland may be in the not too distant future.

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